

HOW BIG AND HOW CLOSE? HABITAT PATCH SIZE AND SPACING TO CONSERVE A THREATENED SPECIES

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ABSTRACT. We present results of a spatially explicit, individual-based stochastic dispersal model (HexSim) to evaluate effects of size and spacing of patches of habitat of Northern Spotted Owls (NSO; *Strix occidentalis caurina*) in Pacific Northwest, USA, to help advise recovery planning efforts. We modeled 31 artificial landscape scenarios representing combinations of NSO habitat cluster size (range 4–49 NSO pairs per cluster) and edge-to-edge cluster spacing (range 7–101 km), and an all-habitat landscape. We ran scenarios using empirical estimates of NSO dispersal dynamics and distances and stage class vital rates (representing current population declines) and under adult survival rates adjusted to achieve an initially stationary population. Results suggested that long-term (100-yr) habitat occupancy rates are significantly higher with habitat clusters supporting ≥ 25 NSO pairs and ≤ 15 km spacing, and with overall landscapes of ≥ 35 –40% habitat. Although habitat provision is key to NSO recovery, no habitat configuration provided for long-term population persistence when coupled with currently observed vital rates. Results also suggested a key role of floaters (unpaired, nonterritorial, dispersing owls) in recolonizing vacant habitat, and that the floater population segment becomes increasingly depleted with greater population declines. We suggest additional areas of modeling research on this and other threatened species.

KEY WORDS: Dispersal model, Northern Spotted Owl, habitat size, habitat spacing, HexSim model, threatened species.

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1. Introduction

1.1. The question of habitat amount and distribution in conservation planning. One of the major questions in conservation is how much and what arrangement of habitat is adequate to provide for population persistence of threatened species. Conservation biology is founded, in part, on research and guidelines pertaining to this question, such as ascertaining the effects of habitat loss and fragmentation, and potential benefits of larger sizes and closer spacing of habitat patches (e.g., Shanahan and Possingham [2009]).

Many recent studies have addressed these questions in various ways. For example, Mezquida and Benkman [2010] found that forest habitat patch size and structure influenced rates of seed consumption by Common Crossbills (*Loxia curvirostra* complex) in the Pyrenees. Cerezo et al. [2010] determined that effects of forest habitat area and fragmentation on dispersal regulated the occurrence of birds in Guatemala. Other studies have found that amount and arrangement of habitats affect species abundance, distribution, and ecological functions (e.g., Loehle [2007], Keitt [2009]).

The question of how much habitat is enough to meet conservation goals should be answered with scientific rigor designed to clearly specify measurable objectives and to identify knowledge gaps (Tear et al. [2005]). We modeled potential effects of habitat patch size and distribution on persistence of a threatened species of owl to provide a basis for establishing measurable habitat management objectives and to identify areas of variation and uncertainty of population response.

1.2. Northern Spotted Owls under threat. In 1990, USDI Fish and Wildlife Service (FWS) listed the Northern Spotted Owl (NSO; *Strix occidentalis caurina*) as a threatened species under the Endangered Species Act (USFWS [1990]). Since that time, several sets of conservation guidelines and draft recovery plans have been developed that focus largely on conservation and restoration of mature and old-growth conifer forest as key habitat for the owl (Thomas et al. [1990], USFWS [1992], Lint [2005]; see Marcot and Thomas [1997] for review). Central issues among such plans have been the amount and distribution of NSO nesting, roosting, and foraging habitat (hereafter, habitat) that would help ensure long-term persistence of NSO populations. In this paper, we define a habitat patch as the amount of mature and old-growth forest used by a territorial pair of NSOs to establish a home range, a habitat cluster as ≥ 2 contiguous habitat patches, and spacing of clusters measured as their nearest edge-to-edge distance.

In 1994, Lamberson et al. (hereafter, LNVN) published results of modeling effects of habitat cluster size and spacing on NSO habitat occupancy, concluding that NSO populations could persist with clusters of sufficient size to support ≥ 20 –25 NSO pairs, spaced no further than the median NSO juvenile dispersal distance (approximately 19 km) as measured between nearest cluster edges (also see McKelvey

et al. [1993]). Subsequent studies determined and confirmed that habitat loss and fragmentation account for a significant portion of the continued declines in NSO populations (Akçakaya and Raphael [1998], Lint [2005]).

1.3. Revisiting the question of habitat size and spacing. Results from LNVN figured prominently in federal agency guidelines on size and spacing of NSO habitat. More recently, FWS has embarked on a revision of their draft NSO recovery plan, and FWS managers required confirmation or new guidance on size and spacing of habitat clusters to ensure long-term persistence of NSO populations that would provide for stability of numbers through successful dispersal and recolonization of habitat. Thus, we were motivated to update the previous modeling efforts to determine how big and how close NSO habitats could be to help provide for the species' conservation and recovery. Our objective was to provide results of modeling NSO population dynamics of reproduction, dispersal, and occupancy to inform FWS on potential effects on NSO population persistence of habitat cluster size and spacing, and to compare our findings to those of LNVN.

2. Simulation modeling methods. We used HexSim, a spatially explicit dispersal model, to simulate NSO use of a series of habitat configuration scenarios. We developed 31 artificial landscapes representing combinations of NSO habitat cluster size (4, 9, 25, 36, and 49 owl pairs) and edge-to-edge cluster spacing (7, 15, 29, 52, 74, and 101 km), and an all-habitat landscape (Fig. 1a). We parameterized the model with known NSO demographic vital rates for stage class-specific reproduction, survivorship, and dispersal distances and dynamics. We tested model parameters and assumptions to determine appropriate model run designs, and analyzed model results in terms of expected habitat occupancy rates and population size and trend (overall finite rate of population change, λ) under each habitat scenario. (See Supplementary Appendix for details of model development and operation.)

3. Results

3.1. Effect of habitat cluster size and spacing. As anticipated, simulation results suggested that the proportion of habitats occupied by NSOs: (1) is greater with larger habitat clusters, (2) is greater with habitat clusters more closely spaced, and (3) declines over portions or all of the 100-year simulations (Fig. 2). Long-term occupancy rates of habitats were significantly higher in scenarios with habitat clusters supporting ≥ 25 NSO pairs and ≤ 15 km spacing. In these scenarios, occupancy ranged 10–40% higher than in the scenarios with only 4- and 9-pair clusters, at various distances, and achieved relatively long-term stability although with highest habitat occupancy rates less than 80% (Fig. 3). At 100 years, occupancy rates of habitat clusters supporting < 10 NSO pairs and > 25 km spacing ranged from

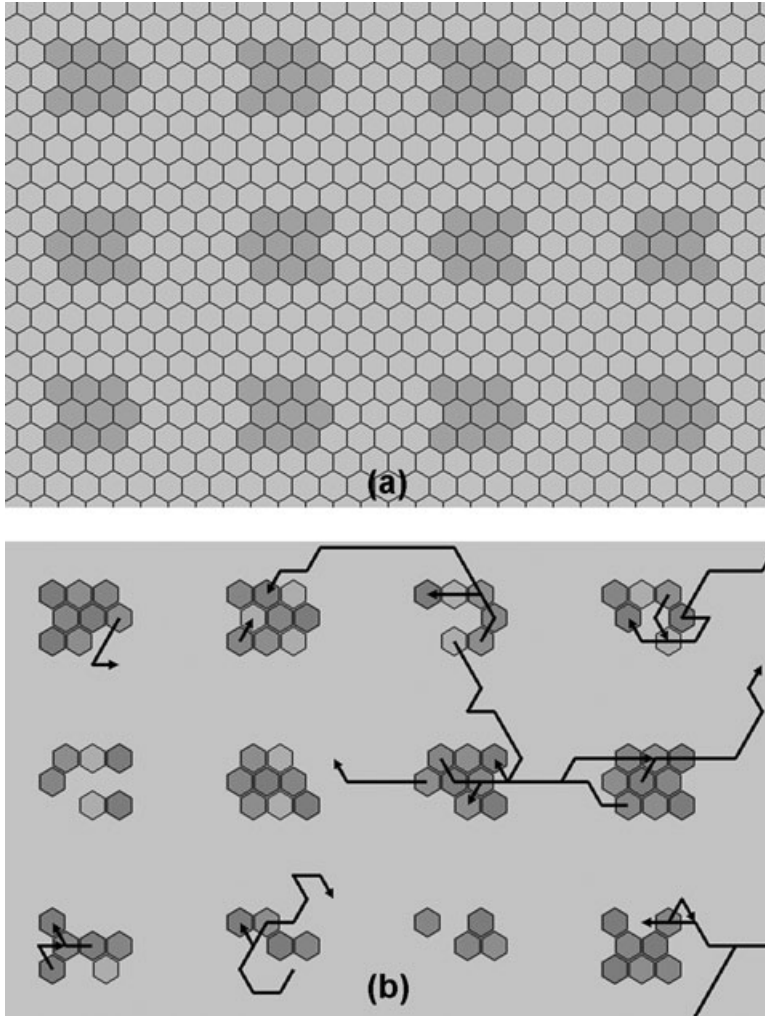


FIGURE 1. Portion of an example landscape as depicted in the HexSim modeling shell, for habitat clusters each capable of supporting 9 pairs of NSOs, and spaced 15 km (4 hexagons) apart (see habitat scenario 8, Supplementary Appendix). Each hexagon represents 1800 ha. (a) Dark hexagons each depict habitat quality and amount suitable for a nesting pair of owls; light hexagons depict unsuitable conditions for nesting but suitable for temporary dispersal in the intervening matrix. (b) Example of one annual time step in a stochastic simulation of owl habitat occupancy and owl movement. Hexagons depict habitats currently occupied by an owl pair; arrows depict current dispersal and exploration movements by unpaired owls.

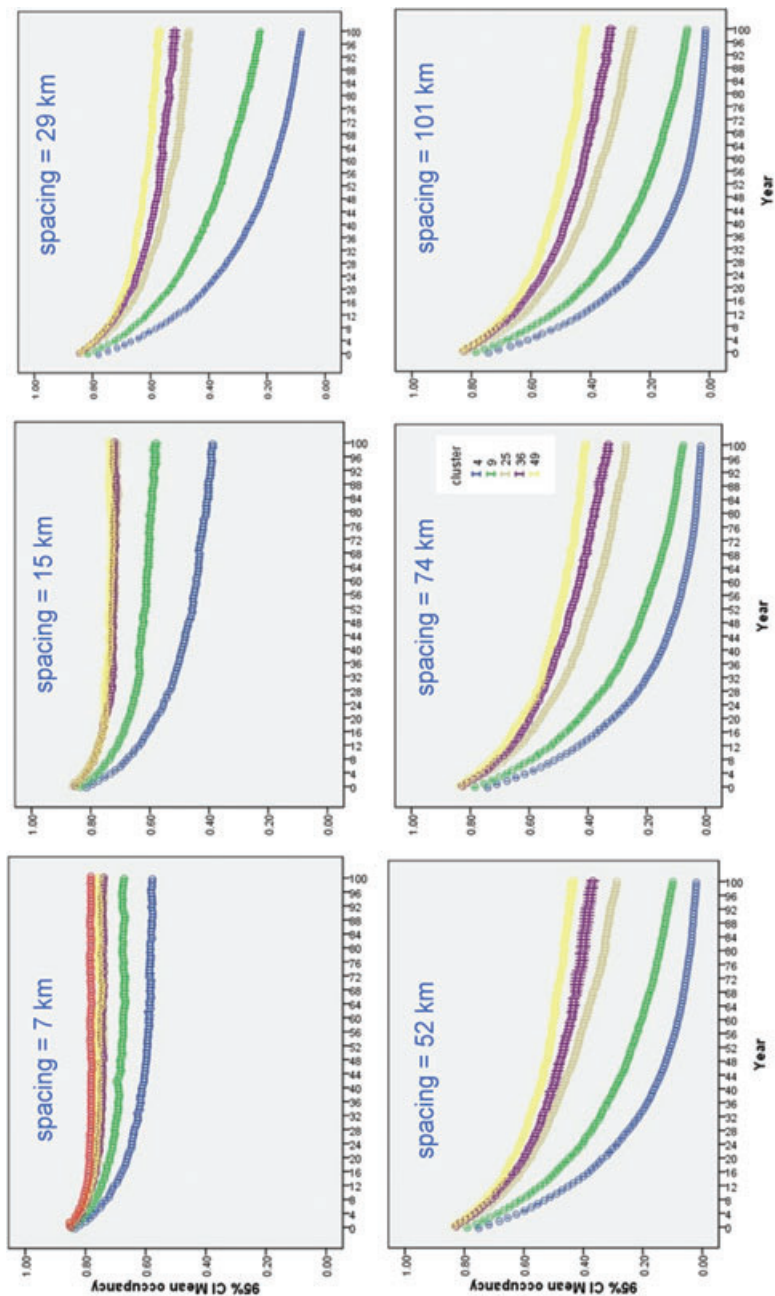


FIGURE 2. Results of habitat occupancy simulations using the HexSim spatially explicit demographic and dispersal model on data from Northern Spotted Owls in Pacific Northwest, U.S., for 30 combinations of habitat cluster size and spacing. Results shown here depict 95% confidence interval of mean occupancy rate of all habitat hexagons (total no. of owl pairs) as a function of simulated time, and used adult stage class survival rates providing an inherently stationary population so that declines in these simulations were entirely from dispersal mortality (see Supplementary Appendix).

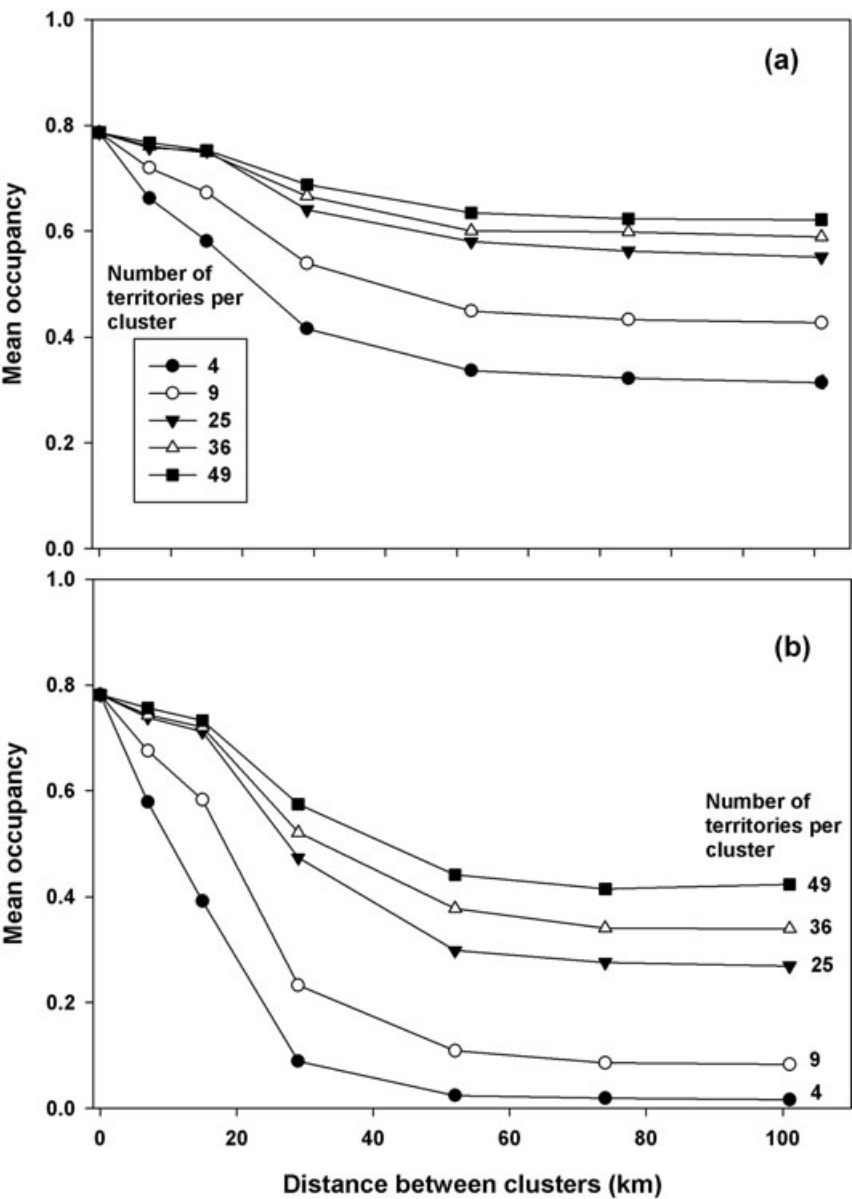


FIGURE 3. Simulation results of mean occupancy of all habitat hexagons (total no. of owl pairs) as a function of distance between habitat clusters, by habitat cluster size (no. territories per cluster), at (a) 20 years and (b) 100 years. Results are based on stationary population demographics. The points at $x = 0$ in both graphs represent the all-habitat scenario.

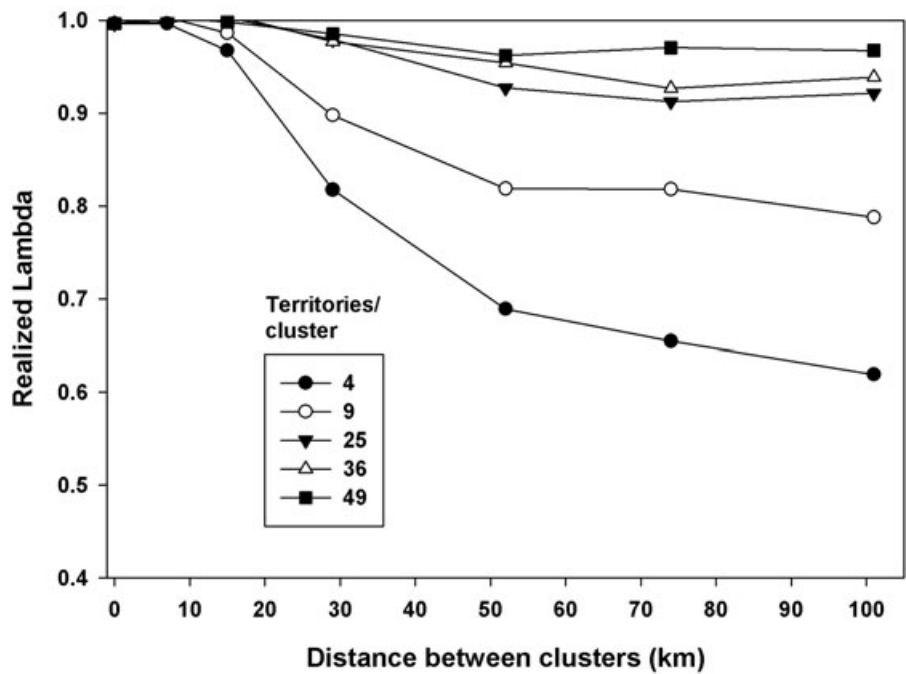


FIGURE 4. Realized λ calculated from simulation runs as the change in total occupied habitats (no. of Northern Spotted Owl pairs) from year 80 to year 100, as a function of habitat cluster spacing and size.

approximately 25% to near zero; under such conditions, long-term viability of NSO populations would be highly unlikely and extinction imminent.

In decades 8–10, realized $\lambda = 1.0$ (stationary population) only under scenarios of habitat cluster size ≥ 25 owl pairs and cluster spacing of ≤ 15 km (Fig. 4). In all other cases, by the end of the century, realized λ was < 1.0 , and was drastically so with smaller and more widely spaced habitat clusters (as low as about $\lambda = 0.6$ with 4-pair clusters). The implication is that, with realized $\lambda < 1.0$, the overall rate of habitat occupancy and simulated population size would continue to decline.

These results were based, however, on use of adult stage-class survivorship adjusted to achieve initially stationary population demographics (see Supplementary Appendix), so as to determine the incremental effect of habitat cluster size and spacing on habitat occupancy and subsequent population trend separate from conditions of adult survivorship. Under demographic rates that reflect current values, occupancy rates under all landscape scenarios declined, often severely, and adverse effects of habitat clusters of small size and wide spacing were greatly magnified.

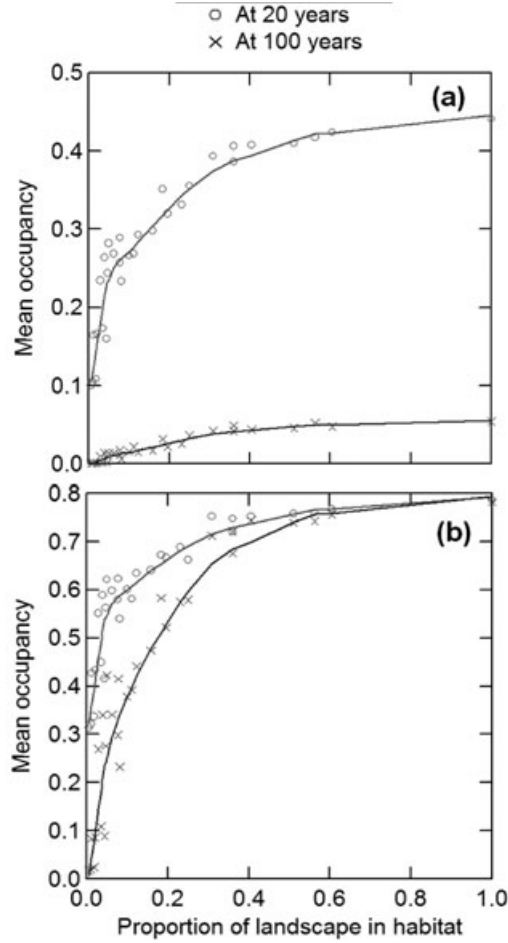


FIGURE 5. Mean occupancy rate of habitat hexagons from all simulation runs as a function of proportion of the landscape in habitat at years 20 and 100, using (a) observed demographic vital rates and (b) adult survivorship adjusted for a stationary population. Each point represents a specific habitat configuration scenario and curves were fit using locally weighted scatterplot (LOWESS) smoothing with tension = 0.5.

3.2. Effect of proportion of the landscape in habitat. Model results suggested nonlinear relationships between mean occupancy and the proportion of the landscape in habitat (Fig. 5). Under actual population demographic conditions (initial $\lambda = 0.95$), short-term (20-year) mean occupancy of habitat remained $<50\%$ under all scenarios, and long-term (100-year) mean occupancy $\leq 5\%$ (Fig. 5a), suggesting eventual population extinction. Under stationary population demographic conditions (initial $\lambda = 1.00$), however, short- and long-term occupancy rates

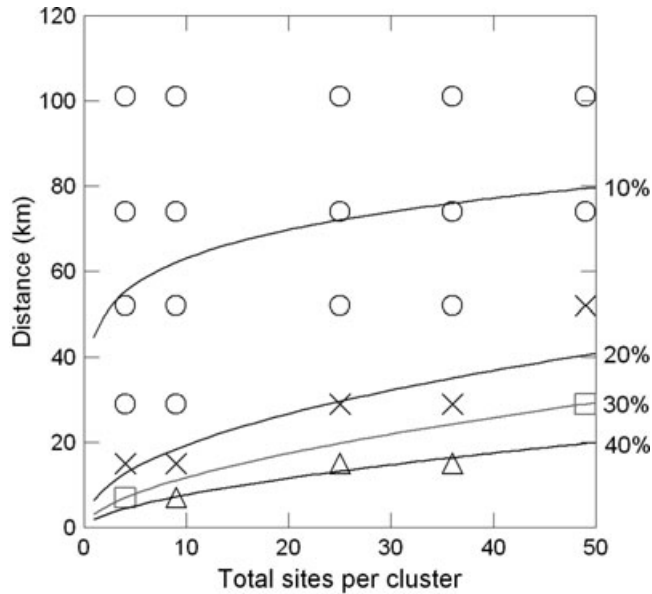


FIGURE 6. Summary of 26 simulated landscapes (selected for comparison with analysis in Lamberson et al. [1994]) consisting of $\leq 40\%$ of the landscape in habitat, with power curves fit to nearest 10% increments.

generally converged at 80% in a landscape of all habitat (Figs. 3 and 5b) and was not 100% because of chance dispersal of owls every time step that temporarily left some sites unoccupied but that quickly refilled in subsequent time steps.

The nonlinear relationship between mean occupancy and proportion of the landscape in habitat also suggested that occupancy began to asymptote when the landscape consisted of about 35–40% habitat (Fig. 5). The various combinations of size and spacing of habitat clusters that produced at least 35–40% of the landscape in habitat (Fig. 6) seemed adequate to provide for successful NSO dispersal and recolonization. This implies that, with $\geq 35\text{--}40\%$ of the landscape in habitat, habitat cluster size and spacing does not matter; however, it could matter very much, as our test landscapes were designed only to test habitat clusters that are evenly spaced. If habitat at a given landscape percentage was to be more contiguously distributed, or more fragmented with wider gaps, than in our contrived habitat dispersion patterns, then mean occupancy may not fit our specific findings. Habitat dispersion patterns can have major consequences on expected occupancy rates (e.g., Loehle [2007]).

3.3. Effect of adult survivorship. As noted above, long-term habitat occupancy and population trends of NSOs are largely dependent on their demographic

vital rates, particularly adult survivorship. Under current estimated mean demographic vital rates with declining populations, no landscape scenario provided for long-term stability or recovery of NSOs. That is, empirical data suggest that NSO populations, as a whole throughout their studied range, are declining, despite the current distribution and amount of habitat (Anthony et al. [2006]). This does not, however, mean that total habitat amount, and habitat cluster size and spacing, are unimportant; adequate amount and proximity of habitat are necessary for population persistence, and observed declines of NSO populations are likely caused by other factors either in isolation or in combination with habitat conditions. Our analysis using stationary population parameters essentially determined the incremental contribution of habitat to population persistence, but habitat alone likely cannot solve the problem of population declines.

3.4. The role of floaters. Floaters constitute the segment of the population consisting of unpaired, nonterritorial birds in dispersal, exploring for unoccupied habitat in which to settle. HexSim tracks the floater segment and our simulations suggested that floaters played a key role in recolonizing habitat and stabilizing population dynamics. In the all-habitat landscape scenario, the number of floaters in the first years of the simulation quickly rose to 40% of the number of birds holding territories and then dropped by year 20 to remain at around 5%.

The total number of floaters, as well as the percentage of the population in floaters, declined as the value of λ decreased (Fig. 7). This suggests that, as a population declines, the floater segment becomes increasingly depleted until they can no longer keep pace with, and recolonize, vacant habitats. The apparent nonlinear relationship (Fig. 7) also suggests increasingly rapid population declines with smaller populations.

3.5. Model tests of dispersal distance. The distribution of simulated dispersal distances compared favorably to known (Forsman et al. [2002]) NSO dispersal distances (Fig. 8). Both suggest approximately lognormal distributions with a mode around 10 km. These HexSim model results matched known NSO dispersal distances well.

4. Discussion and management implications. Our simulation results are most appropriately interpreted in two ways. First, projected levels of NSO habitat occupancy, and population sizes and trends, should be viewed as approximations and in relative terms, comparing outcomes among various habitat cluster sizes and distances. Real-world levels of occupancy and population sizes and trends will assuredly differ from the modeled results, for reasons discussed below. Second, our results using adult survivorship adjusted upward for an initially stationary population were intended strictly to determine the incremental effect of habitat cluster

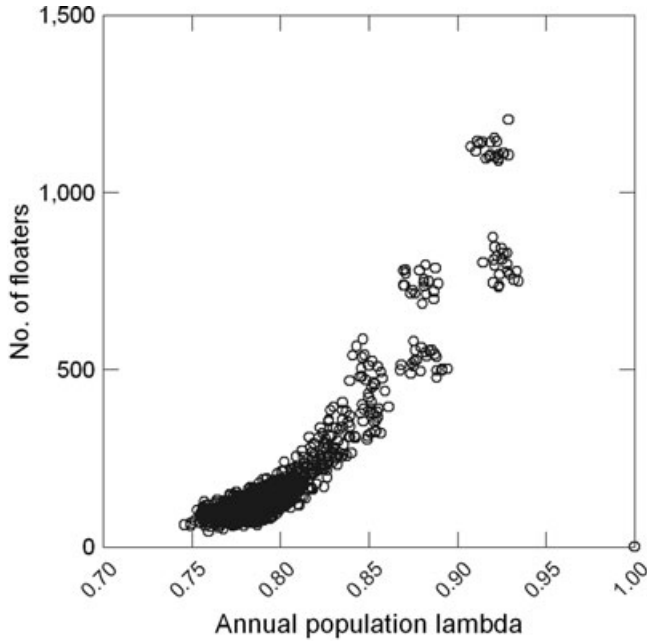


FIGURE 7. Distribution of the proportion of the total population in floaters, as a function of annual population finite rate of change λ , for the all-habitat scenario. Each circle is one annual value over 100 simulated years and 20 replicate runs.

size and distance on population dynamics, not to suggest that habitat alone will ameliorate other population stressors.

4.1. Comparison to previous modeling results. It was not surprising that the general form of our modeling results—that NSO population persistence was greater with larger habitat clusters spaced closer together—matched those of LNVM, as both modeling approaches were based on similar demographic and dispersal dynamics. Our effort, using HexSim, provided greater flexibility (and complexity) in depicting dispersal dynamics (see Appendix) and did not fundamentally discriminate within-cluster dispersal and among-cluster dispersal processes as did LNVM's model. Overall, we view the use of HexSim as a means of verifying and refining LNVM's findings, recognizing that some differences between the two model outcomes are attributable to the model structures and their state parameters. We also constructed our habitat scenarios in part to match those reported by LNVM, to compare our results directly to theirs.

4.1.1. Habitat size, spacing, and occupancy dynamics. Our results on habitat size, spacing, and occupancy dynamics match those of LNVM in general form. For

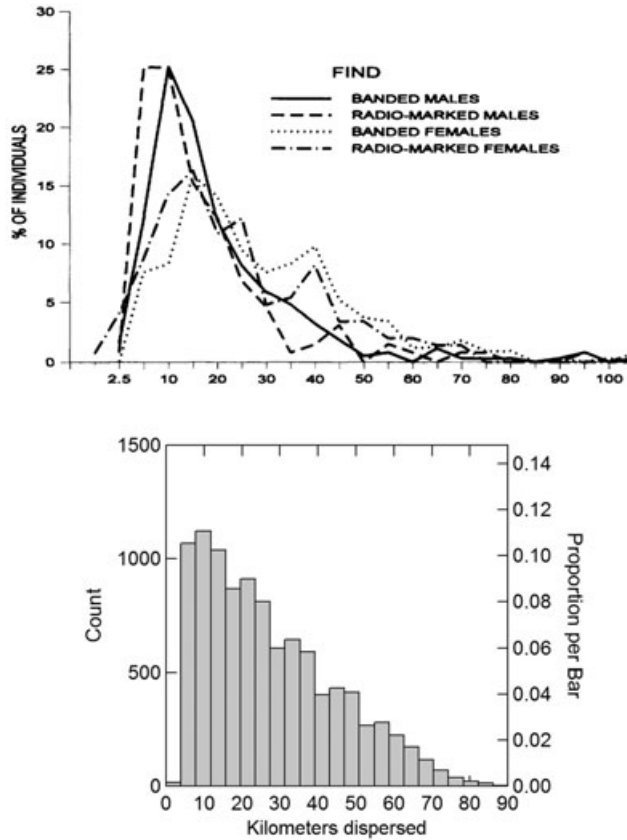


FIGURE 8. Final distance (km) of dispersing Northern Spotted Owls summarized (a) by Forsman et al. [2002] from banded and radio-marked birds and (b) from stochastic simulation model runs using the all-habitat scenario with vital rates adjusted for a stationary population (see Supplementary Appendix).

example, we demonstrated that mean occupancy tends to be lower with small habitat cluster size, greater distance between clusters, and longer simulation time (Fig. 3), just as LNVM reported. Our results suggested that NSO habitat clusters ≥ 25 pairs in size and ≤ 15 km spacing provide for substantially higher mean occupancy rates than do smaller clusters spaced more widely (Fig. 2); similarly, LNVM recommended habitat clusters to support at least 20–25 NSO pairs, with diminishing returns beyond that size, although they did not identify specific distances among clusters that would more likely provide for population persistence. We found that incremental decrease in spacing among habitat clusters had a far greater effect on increasing occupancy rate than did increasing habitat cluster size (Fig. 6); LNVM

likewise suggested, albeit only qualitatively, that preserving connectivity outweighs benefits from increasing size of habitat clusters. Also, based on modeling work by Holthausen et al. [1995] and Raphael et al. [1998], Noon and McKelvey (1996:157) subsequently recommended that “more recent modeling suggests that carrying capacities of perhaps 30–40 pairs per HCA [habitat cluster] are needed.”

We also found that using empirical vital rates often led to greatly declining populations no matter the habitat configuration, so like LNVM, we boosted adult survival to run simulations with initially stationary population growth rates (see Supplementary Appendix). We found that mean habitat occupancy rates typically dropped during approximately the first decade of simulated time (Fig. 2), indicating model start-up bias, as suggested also by LNVM.

However, occupancy levels tended to be lower in our simulations than in LNVM's. This is likely because the HexSim model we used accounted for more real-world NSO parameters than did their model, such as proportion of each stage class dispersing, dispersal distances denoted by stage class, movement and exploration dynamics constrained by dispersal distances, and stage-class specific reproduction values. Our model also constrained owls along the edge of the landscapes, mimicking geographic barriers, whereas those of LNVM were based on a torus geometry which allowed for dispersing owls to wrap around to the opposite edge.

Also, LNVM referred to total number of habitat sites per cluster, but they assumed that only 60% of the habitat in the clusters was suitable, and that all habitat could be occupied (R. Lamberson and B. Noon, personal communication); thus, to compare directly with our results (Fig. 3), the “total sites per cluster” presented by LNVM should be multiplied by 0.6. (see Supplementary Appendix). Our figures showing cluster size do not presume such correction factors, and should be interpreted directly as number of simulated occupied sites.

LNVM reported that clusters of 20 owl pair sites spaced 19 km apart stabilized at about 77% occupancy at 100 years, which was largely corroborated by our findings that clusters ≥ 25 pairs spaced about 19 km apart achieved about 70–75% occupancy at 100 years (Fig. 3b). As with LNVM, our result assumed initially stationary population demographics. Also, Noon and McKelvey [1996] noted: “Subsequent modeling suggests that reserves with a carrying capacity of 20 pairs are stable only if juvenile search efficiency is high and edge effects are minimal. To achieve local stability within the constraints of real landscapes, more recent modeling suggests that carrying capacities of perhaps 30–40 pairs per HCA are needed. In addition, a few large reserves (>100 pairs) significantly safeguard against population extinction. For these reasons, the original reserve design proposed by the ISC (Thomas et al. [1990]) represents a minimum system, with greater risks to persistence than initially envisioned.”

Some differences between our results and those of LNVM might also be attributable to differences in how the dispersal process was modeled. LNVM modeled

dispersal explicitly as a two-step process per time period, where first an NSO would search within a cluster for suitable unoccupied habitat, and if none was found would then search outside the cluster. We modeled such dispersal behavior more implicitly whereby NSO searches for unoccupied habitat was guided by general rules of movement distance and exploration (see Supplementary Appendix) that applied to all habitat scenarios equally.

4.1.2. *Proportion of landscape in habitat.* The geometry of habitat cluster size and spacing is such that, when the landscape consists of $\leq 40\%$ habitat, an incrementally smaller decrease in spacing may provide a greater proportion of the total landscape in habitat than would an incremental increase in cluster size (Fig. 6). These results will figure into broader implications of habitat conservation for threatened species in general.

Our results suggested that occupancy tends to reach about 90% of long-term asymptote levels with about 35–40% of the landscape in habitat, depending on cluster size and spacing scenarios (Fig. 5). LNVN also found that increasing the percent of the landscape in habitat clusters increased mean occupancy. However, their modeled landscapes ranged only to 45% although their results also suggested a convergence of occupancy rates at approximately that percentage especially for landscapes with habitat clusters > 15 owl pairs in size.

4.2. Comparison to NSO habitat management guidelines. Obviously, our contrived landscapes bear little resemblance to real-world distributions of NSO habitat. However, we can compare some of the general lessons learned from our simulations to actual NSO habitat conservation guidelines proposed or instituted on various public lands since 1977 (Table 1).

Guidelines have varied widely, ranging from single-pair sites with unspecified spacing criteria in 1984, to 20+ pair clusters spaced about 20 km apart in a recent FWS Final NSO Recovery Plan. Habitat area specified per NSO pair also greatly increased over the evolution of these guidelines, from 121 ha per pair in 1977 (Thomas et al. [1990]:54) to 4,452 ha per pair in 2008 (on the Olympic Peninsula, Washington; USFWS [2008]:73). Comparing size and spacing values to our analysis (Fig. 3, which presumes that the cause of low adult mortality has been remedied) suggests that the early guidelines (ca. 1977–1988) generally calling for < 4 pairs per cluster variously spaced 10–19 km apart would have provided for no more than about 50–60% habitat occupancy over the short term and at best 30–50% over the long-term; coupled with other known stressors, this would likely have been a formula for extirpation throughout a significant portion of the range. Later guidelines (1990–2008) calling for 20+ pair clusters spaced 19 km apart would fare better, providing for about 60–70% occupancy in the short to long term.

TABLE 1. Summary of Northern Spotted Owl (NSO) habitat guidelines in the Pacific Northwest U.S., focusing on criteria for habitat cluster size and spacing.

NSO guideline and source	Year	Habitat size (no. NSO pairs)	Habitat spacing (km)
Oregon Spotted Owl Management Plan	1977	3–6	13–19
SOMAs (Spotted Owl Management Areas), FS Regional Guidelines	1984–85	1	Unspecified
Spotted Owl Habitat Areas (SOHAs), FS Regional Guidelines	1988	3+ 1	19 10
Habitat Conservation Areas (HCAs), ISC	1990	20	19
Designated Conservation Areas (DCAs; two sizes & distances), FWS NSO Draft Recovery Plan	1992	20 2–19	19 11
Late-Successional Reserves (LSRs), Northwest Forest Plan	1994	20	19
Managed Owl Conservation Areas (MOCAs; two sizes), FWS Final NSO Recovery Plan	2008	20+ 1–19	19 19

Note: FS = USDA Forest Service, Pacific Northwest Region; FWS = USDI Fish and Wildlife Service.

4.3. Implications for recovery of NSOs. As plans continue to be developed for recovery of NSO populations, guidelines for habitat protection and restoration could be crafted with our findings in mind. Our results can be used in three ways: (i) to compare relative levels of NSO habitat occupancy, and population size and trend, among alternative habitat configurations; (ii) given a particular goal for NSO habitat occupancy or population size and trend, the set of habitat configurations that would lead to such outcomes; and (iii) as a basis for more refined modeling

using real-world current and projected future landscapes. We stress that our results are to be viewed only as information to aid and help inform decision-making, not as decision outcomes per se. Also, successful recovery of NSO populations would need to address stressors and conditions other than how big and how close habitats need to be, particularly other influences affecting low adult survival rates.

One aspect of NSO recovery amenable to further modeling may pertain to the dynamics of the floater segment of the population that might play a key role in refilling vacant habitat. In other bird species, such as *Bubo* owls, floaters can have a salient influence on population demography (Rohner [1996]) and provide for long-distance dispersal (Aebischer et al. [2010]). Understanding the conditions under which floaters can persist and contribute to a sustainable population might be one facet of species recovery not typically addressed in conservation plans.

We modeled only the effects of habitat architecture on NSO persistence. Other stressors have come to light since the early 1990s that likely have contributed to declines in NSO populations, namely competitive exclusion by invading Barred Owls (*Strix varia*). To this end, conservation of NSO populations cannot be expected to succeed based only on habitat provision, but habitat will be an essential component of NSO recovery.

4.4. Broader implications for other species and issues. Clearly, population persistence is aided by a greater amount of habitat that is less fragmented and with larger habitat patches more closely spaced, than by opposite conditions. Precise amount, size, and spacing of habitats to provide particular persistence outcomes are species-specific.

What is less clear is the proportion of the landscape in habitat that would provide for persistence. Using a discrete reaction-diffusion modeling approach, Flather and Bevers (2002) reported that when landscapes contained at least 30–50% habitat, habitat amount mostly determined persistence, but below this percentage habitat arrangement became important because of dispersal mortality. Our study also suggested that, above about 35–40% of the landscape in habitat, owl numbers and habitat occupancy approached an asymptote and habitat arrangement parameters of size and spacing had less effect on persistence than they did at lower landscape percentages. Whether such findings would hold with other species under various environmental conditions may require additional modeling and research.

Further, representing only females in HexSim means that it cannot simulate inter-gender, intraspecific interactions or Allee effects that might arise from difficulties in locating mates. Also, although HexSim is flexible in allowing changes in the underlying habitat map over time during a simulation run, our habitat maps remained static to compare long-term effects of various habitat patch architectures.

4.4.1. Research questions. Modeling constructs that explore habitat configurations suggest an array of opportunities for areas of research and for considering

other ecological conditions that affect threatened species persistence. Our approach can be modified—specifically the parameters pertaining to demographic vital rates, habitat quality, and dispersal, exploration, and movement functions—to investigate the influence of habitat patterns on a wide variety of other species. The following research questions inspired by our findings could be modeled on species with various degrees of vagility, habitat specificity, and life history characteristics:

- (i) whether expected rates of habitat occupancy are influenced more by spacing among habitat clusters than by habitat cluster size;
- (ii) whether spacing among habitat clusters provides a greater proportion of the total landscape in habitat than would be provided by an incremental increase in cluster size;
- (iii) the role of dispersed, large habitat clusters as potential source habitats (e.g., as suggested for NSOs by Noon and McKelvey [1996]; also see Alderman et al. [2005]);
- (iv) the influence of geographic features as dispersal barriers or filters;
- (v) the influence of competitors and predators on site occupancy and population persistence;
- (vi) the incremental contribution of habitat corridors of specific locations and widths, to long-term habitat occupancy and population size and trend;
- (vii) determination of most-used dispersal and travel routes through a landscape;
- (viii) effect on occupancy from disturbance events on, and stochasticity of, habitat quality (Bascompte et al. [2002]);
- (ix) the dynamics of the floater segment of the population and their contribution to overall population persistence; and
- (x) the degree to which extinction risk rises with increasingly smaller population size, as has been reported in other simulation modeling (O’Grady et al. [2004]) and population viability analyses of endangered species (Morrison et al. [1992], Reed et al. [2003]).

Results from HexSim modeling could be compared with those generated from alternative approaches to modeling spatially explicit dispersal dynamics, such as with use of: least-cost analysis to evaluate wildlife habitat linkages (LaRue and Nielsen [2008], Beier et al. [2009]); resource selection functions (Chetkiewicz and Boyce [2009]) and landscape genetics (Cushman et al. [2006], Epps et al. [2007]) to delineate movement corridors; circuit and network theory to evaluate effects of habitat connectivity (McRae et al. [2008], Phillips et al. [2008], Lookingbill et al. [2010]); optimal foraging theory to determine movement patterns (Skórka et al. [2009]); habitat patch isolation metrics to predict dispersal movements (Bender et al. [2003]); and other modeling approaches (e.g., Hargrove et al. [2005], BenDor et al. [2009], Nicol and Possingham [2010]). Results also could generate hypotheses

on broader implications of, and as a step toward a generalized approach for, habitat conservation for threatened species.

4.4.2. Considerations for further modeling of disturbance factors. Real-world population response of NSOs (and other threatened species) is subject to a wide array of other factors not considered in our modeled landscapes. Such factors, that might be worked into future modeling efforts, include influence of variability in weather (LaHaye et al. [2004]), climate change (Carroll et al. [2010]), stand-replacing fires (Kennedy and Wimberly [2009]), forest thinning and silviculture (Andrews et al. [2005], Lee and Irwin [2005]), incursion of NSO habitat by Barred Owls (Pearson and Livezey [2007]), and direct influence of habitat condition on demography (Dugger et al. [2005]). Opportunities seem wide open for extending our modeling approach in many fruitful directions, any of which could provide valuable new information to guide research and conservation planning for this, or other, threatened species.

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SUPPORTING INFORMATION

The following supporting information is available for this paper.

TABLE S1. Characteristics of the 31 simulated landscapes varying Northern Spotted Owl (NSO) habitat cluster size and spacing as used in the HexSim simulation model.

TABLE S2. Northern Spotted Owl reproduction and survivorship rates used in the HexSim model.

TABLE S3. Final dispersal distances from banded Northern Spotted Owls as summarized from Forsman et al. [2002] and used in the HexSim model expressed as number of hexagons (1 hexagon = 1,800 ha and is 4,559 m wide).

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SUPPLEMENTARY APPENDIX. Methods for modeling Northern Spotted Owl dispersal.

Marcot, B. G., M. G. Raphael, N. H. Schumaker, and B. Galleher. 2012. How big and how close? Habitat patch size and spacing to conserve a threatened species. *Natural Resource Modeling*

METHODS

Spatially-explicit dispersal model. We used HexSim (version 1.2.1.5), a spatially-explicit, individual dispersal simulation modeling shell developed by N. Schumaker (www.epa.gov/hexsim/), to model NSO population response to artificial landscapes with varying habitat cluster size and spacing dimensions and varying proportion of the total landscape in habitat. HexSim is the current generation of the model previously called PATCH. Applications of PATCH to a variety of habitat and species evaluation projects have appeared in at least 20 peer-reviewed articles (e.g., Rustigian et al. 2003, Schumaker et al. 2004). In our use of HexSim, reproduction and dispersal were represented as stochastic events. Events of reproduction, dispersal, exploration, establishing a territory (where appropriate), and survival were conducted for each simulated year, and locations of territorial and non-territorial (floater) individuals (females) were tracked and tallied for each time period (year).

Landscape scenarios. A HexSim map consists of a tiled plane of hexagons. In our simulated landscapes, each hexagon was a single patch which was either fully suitable NSO habitat or fully unsuitable, and represented 1,800 ha (4,559 m side-to-side width) which is the median amount of habitat used by a breeding pair of NSOs (USFWS 2008).

The two variables in our simulated landscapes were habitat cluster size and spacing between habitat clusters. A habitat cluster consisted of contiguous hexagons of habitat that would provide for multiple pairs of NSOs. Habitat clusters were shaped to be as compact as possible within the hexagon configuration. Using ArcInfo Workstation (ESRI 1982-2008), we developed 31 artificial landscapes representing combinations of NSO habitat cluster size (4, 9, 25, 36, and 49 owl pairs) and edge-to-edge cluster spacing (7, 15, 29, 52, 74, and 101 km), and an all-habitat landscape (Supplementary Appendix Table 1). We selected these habitat cluster sizes and spacing values to bracket and best match those used by LNVN and as needed for consideration by FWS, and also to include an all-habitat landscape as a control condition. We held the total amount of habitat constant and varied the size of the overall landscape to accommodate the cluster size and spacing parameters. This also served to vary the total proportion of habitat throughout the landscape, which we related to population persistence.

Supplementary Appendix Table 1. Characteristics of the 31 simulated landscapes varying northern spotted owl (NSO) habitat cluster size and spacing as used in the HexSim simulation model.

Habitat cluster size			Spacing between habitat clusters		Landscape parameters				
Habitat scenario	Hectares of NSO habitat per cluster	No. suitable NSO sites (hexagons) per cluster	Km	No. hexagons	Total no. of habitat clusters	Total no. suitable NSO sites (suitable hexes)	Total area of suitable NSO habitat (ha)	Total no. hexagons	Percent of landscape in suitable NSO habitat
1	7,200	4	7	2	441	1,764	3,175,200	7,056	25%
2	7,200	4	15	4	441	1,764	3,175,200	15,876	11%
3	7,200	4	29	7	441	1,764	3,175,200	39,900	4%
4	7,200	4	52	12	441	1,764	3,175,200	98,784	2%
5	7,200	4	74	17	441	1,764	3,175,200	176,800	1%
6	7,200	4	101	23	441	1,764	3,175,200	308,112	1%
7	16,200	9	7	2	196	1,764	3,175,200	4,900	36%
8	16,200	9	15	4	196	1,764	3,175,200	9,604	18%
9	16,200	9	29	7	196	1,764	3,175,200	21,714	8%
10	16,200	9	52	12	196	1,764	3,175,200	49,980	4%
11	16,200	9	74	17	196	1,764	3,175,200	86,829	2%
12	16,200	9	101	23	196	1,764	3,175,200	147,378	1%
13	45,000	25	7	2	72	1,800	3,240,000	3,528	51%
14	45,000	25	15	4	72	1,800	3,240,000	5,832	31%
15	45,000	25	29	7	72	1,800	3,240,000	11,336	16%
16	45,000	25	52	12	72	1,800	3,240,000	23,408	8%
17	45,000	25	74	17	72	1,800	3,240,000	38,407	5%
18	45,000	25	101	23	72	1,800	3,240,000	62,248	3%
19	64,800	36	7	2	49	1,764	3,175,200	3,136	56%
20	64,800	36	15	4	49	1,764	3,175,200	4,900	36%
21	64,800	36	29	7	49	1,764	3,175,200	9,016	20%
22	64,800	36	52	12	49	1,764	3,175,200	17,640	10%
23	64,800	36	74	17	49	1,764	3,175,200	28,512	6%
24	64,800	36	101	23	49	1,764	3,175,200	45,248	4%
25	88,200	49	7	2	36	1,764	3,175,200	2,916	60%
26	88,200	49	15	4	36	1,764	3,175,200	4,356	40%
27	88,200	49	29	7	36	1,764	3,175,200	7,650	23%
28	88,200	49	52	12	36	1,764	3,175,200	14,364	12%
29	88,200	49	74	17	36	1,764	3,175,200	22,765	8%
30	88,200	49	101	23	36	1,764	3,175,200	35,442	5%
31	5,891,400	3,273	0	0	1	3,273	5,891,400	3,273	100%

Demographic rates. We parameterized HexSim with estimates from empirical studies on NSO biology, principally on stage-class survivorship and reproduction (Anthony et al. 2006) and stage-class dispersal (Forsman et al. 2002). We consulted directly with previous modelers Rollie Lamberson, Kevin McKelvey, and Barry Noon to ensure that our modeling approach best

matched their modeling assumptions and methods, and with NSO biologists Robert Anthony and Eric Forsman to ensure correct model parameterization of vital and dispersal rates. To facilitate comparison among the various landscape configurations, we did not vary inherent vital and dispersal rates by habitat configurations (size and spacing of habitat clusters), nor were empirical data available by which to provide a basis for such variation.

Reproduction and survivorship. To parameterize HexSim, which we used as a female-only model, we summarized NSO stage-class specific reproduction b and survivorship s from a published meta-analysis that combined results from 14 demographic studies across the range of NSOs in Pacific Northwest, U.S. (Anthony et al. 2006), using 4 stage classes (Supplementary Appendix Table 2).

Supplementary Appendix Table 2. Northern spotted owl reproduction and survivorship rates used in the HexSim model.

		Reproduction		Survivorship		
Stage class	Stage class name	Reprod. class	Value ¹	Survival class	Average ²	Stable
0	juvenile	b_0	0.000	s_0	0.442	0.442
1	subadult, 1-yr-old	b_1	0.078	s_1	0.814	0.814
2	2-yr-old	b_2	0.192	s_2	0.850	0.850
3	3-yr-old	b_3	0.348	s_3	0.856	0.882 ³

¹Females born per female per year.

²Values derived from summary of empirical data for s_0 from A. Franklin (pers. comm.) and for s_1 - s_3 from Anthony et al. (2006) (see text). These values result in population $\lambda = 0.95$.

³Value adjusted to achieve population $\lambda = 1.00$ (see text).

We calculated stage-class reproduction (no. females born per female per year) and annual survivorship as weighted means of values from NSO demographic study areas provided by Anthony et al. (2006), using their estimates of the reciprocal of standard error as weights and excluding data from one NSO demographic study area (Marin County) because of small sample size (R. Anthony, personal communication). The value of the first stage class survival, s_0 , was not available from Anthony et al. (2006) and was provided by A. Franklin (personal communication).

We used the spreadsheet add-in program PopTools (Hood 2009) to calculate overall finite rate of population change, λ , from empirical estimates of mean reproduction and survival, in a standard Leslie matrix formulation:

$$\begin{pmatrix} s_0 b_1 & s_1 b_2 & s_2 b_3 & s_3 b_3 \\ s_0 & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 \\ 0 & 0 & s_2 & s_3 \end{pmatrix}$$

which led to $\lambda = 0.95$, or a declining population. Following the example from LNVM -- who modeled empirical estimates of vital rates that resulted in a declining population no matter the habitat amount and configuration, and vital rates adjusted to achieve a stationary population to better evaluate effects of habitat amount and configuration -- we then increased adult survival (s_3) in PopTools to achieve $\lambda = 1.00$, resulting in a “stationary population” configuration of vital rates (Table 2). We modeled each landscape scenario under the two sets of demographic vital rates representing average (declining) population conditions and stationary population conditions, thus, a total of 62 scenarios combining landscape designs and demographic vital rates.

Dispersal. In HexSim, dispersal paths (Fig. 1b) are generated stochastically based on both path length and autocorrelation of movement direction (Appendix). Path lengths can be constant for all individuals, or drawn from uniform or lognormal distributions. Dispersal consists of a series of steps from a hexagon to one of its six neighbors. Autocorrelation in movement direction is an important consideration in modeling dispersal (Bahn et al. 2008), and in HexSim may be varied between zero and 100%, the higher values representing more linear dispersal paths. Observed dispersal distances, measured straight-line from initial point to final point (referred to in the NSO literature as “final distance”), increase with both total path length and percent autocorrelation.

We parameterized HexSim with empirical data on stage-class specific dispersal distances reported from Forsman et al. (2002) as final distances of banded NSOs (Supplementary Appendix Table 3).

Supplementary Appendix Table 3. Final dispersal distances from banded northern spotted owls as summarized from Forsman et al. (2002) and used in the HexSim model expressed as number of hexagons (1 hexagon = 1,800 ha and is 4,559 m wide).

Stage class	Mean final dispersal distance (km)	Range of final dispersal distance (km)		Mean final dispersal distance (no. hexagons)	Range of final dispersal distance (no. of hexagons)	
		Minimum	Maximum		Minimum	Maximum
0	28.6	1.3	104.6	6.219	0.283	22.744
1	8.2	0.01	63.7	1.783	0.002	13.851
2	6.9	0.17	50.7	1.500	0.037	11.024
3	6.1	0.01	85.2	1.326	0.002	18.526

Dispersal distance and landscape exploration movement for each stage class were bound in HexSim by 0 km on the lower end and actual distances on the upper end. A uniform probability distribution was then used in the model to determine dispersal distance within these value bounds for a given simulated owl, resulting in the simulated dispersal distances being lognormally distributed arising from the stochastic exploration function within the model. We set spatial autocorrelation to a moderate value (50%) to avoid a completely random walk, that is,

to constrain stochastic movement pathways without unduly impeding movement into adjacent hexagons, to match observed dispersal patterns of NSOs (Forsman et al. 2002).

Following each dispersal component (a more or less linear motion; see next section) of a HexSim movement was an exploration event (a local search). Exploration is the process whereby an owl would prospect for suitable vacant habitat to colonize. In this process, our simulated owls could search up to the number of hexagons representing the annual movement space for a given stage class. If a suitable site could not be located and colonized, then the disperser would remain a floater for that time increment, and in the next increment continue exploration for a suitable vacant hexagon.

We also parameterized HexSim with estimates of the proportion of each NSO stage class dispersing. This was a refinement over LNVN's approach which apparently presumed that 100% of each stage class dispersed if not part of a territorial pair. We assumed that 100% of juveniles (stage class 0) dispersed (E. Forsman, personal communication) and calculated annual percent of stage classes 1-3 dispersing to be 21.7, 14.4, and 4.4%, respectively, as sample-size weighted means among birds with various previous mate status (Forsman et al. 2002, see their Table 7).

HexSim model's dispersal and exploration functions. Movement routines in HexSim have two principal parts called *dispersal* and *exploration*. The dispersal component moves individuals across landscapes, but does not allocate resources to them. During exploration, individuals prospect for a vacant suitable site to colonize. Dispersal decisions are based strictly on habitat quality, whereas exploration behavior is influenced by both habitat quality and resource availability. Both dispersal and exploration involve taking individual steps between adjacent hexagons. Individuals never jump to non-adjacent target sites.

Each disperser is assigned a path length. Path lengths are the number of steps that the disperser will move. Path lengths can be constant, or can be drawn from uniform or lognormal distributions. Path length parameters are all specified as number of hexagons. The path length defines how many steps (from one hexagon to a neighbor) each individual will move during a given time increment.

Stopping conditions, if met, will cause an individual to stop its dispersal prior to moving the full path length. The dispersal stopping criteria are specified with a mean resource quality threshold that, if encountered over a specified number of sequential steps, will halt dispersal. The intent is that both the mean quality and amount of resource encountered (the number of steps the mean is taken over) will figure into decisions to abort the dispersal process. Because dispersal does not address resource availability, many dispersers may elect to stop in the same general location. In such cases, only a fraction may be successful at claiming a territory during exploration.

Dispersal behavior is controlled by three parameters: repulsion, attraction, and autocorrelation. Repulsion and attraction pertain to the degree to which a dispersing individual avoids or seeks, respectively, hexagons with particular habitat or resource attributes. The autocorrelation parameter makes dispersal paths more or less random. In the absence of repulsion and attraction, zero auto-correlation produces a uniformly distributed random walk of movement directions. At the other extreme, 100% auto-correlation results in straight-line movement trajectories. However, repulsion, attraction, and auto-correlation all work together to determine the dispersal path characteristics. In spotted owls, repulsion might be used to impose a degree of unwillingness to disperse across urban areas, whereas attraction might be used to

draw owls towards patches of older forest. In our simulations, we provided for a slight attraction to habitat patches that would serve to increase the probability that owls would move to a habitat patch when starting from an adjacent, non-habitat hexagon. We did not use repulsion.

Ignoring landscape boundaries, each hexagon has six neighbors. Taking a single dispersal step involves selecting one neighbor and moving to it. Each neighbor is assigned a value PZ , where P is set based on autocorrelation, and Z reflects any repulsion or attraction. Hexagons can be either repulsive, neutral, or attractive. Autocorrelation probability values P range $[0,1]$, and $0 \leq Z < 1$ if a hexagon is repulsive, $Z = 1$ if it is neutral, and $Z > 1$ if a hexagon is attractive. Once PZ has been computed for each neighbor, the values are normalized by dividing each by the sum. Thus, each neighboring hexagon is ultimately assigned a probability that captures both auto-correlation and the influence of attraction or repulsion. To select a neighbor, a random number is drawn compared to the individual neighbor probabilities (the normalized PZ values). The larger a neighbor's probability, the greater the likelihood that it will be selected.

Auto-correlation is implemented by assigning higher likelihoods to directions that represent forward movement. HexSim therefore constantly tracks the direction of past movements. The abbreviations DA, AL, AR, BL, BR, and DB are used to label the neighbors that are directly ahead, ahead left, ahead right, behind left, behind right, and directly behind. These labels are relative to the forward direction. HexSim uses a “trend period” parameter to better define the forward direction. The trend period is a number of steps selected by the user, and HexSim tracks the forward direction for each step in this period. For example, if the trend period is set to 5, then the forward direction will be stored for each of the last 5 steps. The forward direction actually used to label the six neighbors (that is, locate DA, DB, etc) will be the direction that occurs most frequently over the trend period. The use of trend periods adds a kind of momentum to highly autocorrelated dispersal paths.

Once the DA, AL, AR, BL, BR, and DB labels have been attached to the appropriate neighbors, then each is assigned an autocorrelation probability, P . The equations used to assign P values are as follows:

$$P(DB) = \alpha^4 / 6 ,$$

$$P(BL) = P(BR) = \alpha^2 / 6 ,$$

$$P(AL) = P(AR) = \alpha(2 - \alpha)^{2.467} / 6 , \text{ and}$$

$$P(DA) = 1 - P(AL) - P(AR) - P(BL) - P(BR) - P(DB) ,$$

where

$$\alpha = 1 - (\text{percent autocorrelation}) / 100.$$

These six autocorrelation probabilities are continuous and sum to one. The expressions for $P(AL)$ and $P(AR)$ are designed so $P(DA) = P(AL) + P(AR)$ when the autocorrelation parameter is set to 50%. This is, of course, arbitrary. The formulas for P given above were selected because they satisfied the following four criteria: only a single autocorrelation parameter is required; all solutions must lie in $[0, 1]$; all solutions must be equal when $\alpha = 0$; $P(DA)$ must be 1 when $\alpha = 100\%$. These functions were not based on any particular species' movement pattern, but instead were kept general so that a range of dispersal behaviors could be simulated..

Repulsion and attraction produce a coefficient (Z) which is multiplied by the autocorrelation probability, P . A single hexagon can be either repulsive, attractive, or neutral (neither repulsive or attractive), and this determination is based strictly on its quality score. HexSim hexagon quality scores are strictly non-negative. But attraction and repulsion minimum and maximum parameters can be assigned any real value. For hexagons with a score less than the maximum repulsion, Z is fixed at zero. As the hexagon's score increases from the maximum

to minimum repulsion, Z increases linearly from zero to one. Z remains at one until the hexagon's score increases to the minimum attraction value. When the hexagon's score increases from the minimum to maximum attraction value, Z increases linearly with slope $1/\beta$, where β is the minimum attraction parameter. For hexagon scores greater than the maximum attraction, Z is fixed at χ/β , where χ is the maximum repulsion.

Finally, the probability of moving into each of the six neighboring hexagons is derived by normalizing the individual PZ values. Because the repulsion and attraction parameters may be set outside the range of observed hexagon scores, no hexagon may necessarily ever be fully repulsive or attractive. In fact, all hexagons may easily be set neutral.

The exploration process involves an intensive search for resources. A maximum explored area is specified, in hexagons. Individuals will not be allowed to explore more than this number of hexagons during any single exploration event. Users must also set an exploration goal, such as starting a new group (territory construction; in our use of HexSim, a “group” refers to a territorial female) or joining an existing group. Some goals have primary and secondary components. In these cases, if the primary goal cannot be met, then an attempt is made to attain the secondary goal. Because spotted owls do not form social groups, our simulated owls always attempted to start a new “group” (single-pair territory) and they did not have a secondary goal.

The exploration process can be conducted using one of three exploration algorithms: uniform, greedy, and adaptive. These algorithms are the methods used to select which hexagon to explore. The starting point of each exploration is the individual's location, which is typically the end point of dispersal. As hexagons are explored, they are added to the current explored area. Only immediate neighbors of the already explored hexagons may be visited. Thus, explored areas expand incrementally.

Under the “uniform” exploration algorithm, the closest unexplored neighbor to the exploration starting point will always be selected. Ties are settled randomly. This algorithm tends to produce roughly circular explored areas. Still, the landscape edges, excluded areas, and barriers must be respected. So the ultimate search area may not be a simple set of concentric rings.

The “greedy” strategy keeps track of every hexagon that has been explored, and every unexplored hexagon that touches an explored hexagon. The list of unexplored hexagons neighboring explored ones is prioritized at every step, and the best neighbor is always the next site to be explored. Again, landscape boundaries, excluded areas, and barriers are all taken into consideration.

The “adaptive” exploration strategy is a bit more complex. When it is used, individuals build up a list of already explored hexagons. To select a new site to explore, the adaptive strategy first picks a seed site from the list of already explored hexagons. This seed hexagon is selected probabilistically, based on quality. Then each of the seed hexagon's neighbors is considered for exploration. These neighbors are evaluated based both on their quality and on the number of previously explored neighbors they have. The reason for including the number of previously explored neighbors in the evaluation is that it helps keep the ranges compact. The number of explored neighbors is simply used as a coefficient for the hexagon score. Unexplored hexagons with 1, 2, 3, 4, 5, and 6 explored neighbors are assigned coefficients of 1.0, 1.2, 1.4, 1.6, 1.8, and 2.0, respectively. Finally the neighbor of the seed hexagon having the largest product of score and compactness coefficient is added to the explored area. The adaptive strategy is intended to provide a more sophisticated search than the uniform strategy, while not requiring the limiting assumptions of the greedy approach.

As the exploration process proceeds, individuals continually evaluate their explored areas to see if their goals can be met. When they can, the exploration will stop, and the resources claimed. When they cannot, the explorer will remain a floater.

Tests of model parameters and assumptions. Before conducting the full simulation runs, we first tested and resolved a number of aspects of HexSim model behavior to ensure correct model parameterization (denoted below in parentheses), including determining:

- the most appropriate means of varying landscape designs: viz., keeping the total number of habitat hexagons (approximately 1,800) and the total landscape area of habitat (approximately 3.2 million ha) as constant as the layout geometry would permit, rather than keeping the landscape area (total number of all hexagons) or the number of habitat clusters constant, so that the scenarios could vary in the proportion of the total landscape in habitat (Supplementary Appendix Table 1);
- minimum size of the modeled landscapes (>5 million ha or > 2,900 hexagons) so as to be large enough to avoid bias of boundary effects in the model;
- number of years to simulate in the model to achieve long-term stability of habitat occupancy under stable demographic and all-habitat conditions, determined by plotting running standard error of total occupied sites and noting the asymptote (100 years per run);
- number of model replicates to stabilize variation among model runs (20 replicates per scenario);
- number of simulated years required for the model to correctly initialize and to avoid start-up bias (5 years); and
- the appropriate statistical distributions of simulated dispersal distances (to match empirically reported findings).

We also verified that running the model with a fixed initial seed produced results comparable to using a random initial seed (the former approach providing results that could be duplicated).

Analysis of model outcomes. For each of the 62 modeled scenario combinations of habitat cluster size, habitat cluster spacing, and adult survivorship (λ), we used SPSS 16.0 (Norusis 2007) and SYSTAT (v. 11) (SYSTAT 2004) to summarize output from the HexSim model to produce statistics and graphs displaying (1) expected occupancy rates of habitat sites by (territorial female) NSOs and (2) realized λ , by 20-year time intervals (over 100 years), cluster size, cluster spacing, and proportion of the landscape in habitat. We calculated realized λ from the simulation runs as: $\lambda_{t+k} = N_{t+k} / N_t$, using several different time periods (decades) for t , and where N = total number of occupied sites (NSO pairs, excluding unpaired "floater" individuals) in the simulations at the given decadal time periods. Realized λ is thus the cumulative change in occupied sites from one or more decades before the end of the simulated time series to the end of that time series, and is calculated as the ratio of number of occupied sites at the end of the time period to number at the start of that period.

We summarized findings in terms of effects of habitat cluster size and spacing on short (20-year) and long (100-year) term trends of NSO populations, compared our results to those of LNVN, and considered general implications for habitat conservation guidelines for threatened species.

SUPPLEMENTARY APPENDIX LITERATURE CITED

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